CRETACEOUS DINOSAURS OF AFRICA: EXAMPLES FROM CAMEROON AND MALAWI

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Africa became progressively isolated during the middle portion of the Cretaceous Period as it rifted apart from other Gondwana continents and the southern Atlantic Ocean was completed. Within this geological context, which controls the occurrence and distribution of Cretaceous fossil localities over most of Africa, there is considerable variety in composition and occurrence of fossils. In the Koum Basin of Cameroon in western Africa, abundant footprints of five morphotypes, but scrappy skeletal remains and teeth of the ornithopod *Ouranosaurus* and other taxa are found. In the Karonga area of northern Malawi, in southeastern Africa, more complete skeletal remains are known, including the sauropod *Malawisaurus*, which shows affinity to South American titanosaurids, and an undescribed sauropod taxon. These may demonstrate a range of morphological diversity in sub-Saharan Cretaceous sauropods comparable to that found in South America. ☐ *Cretaceous, Africa, Sauropoda, palaeobiogeography, crocodilia, stratigraphy.*

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Africa is a vast continent with a sporadic fossil record, remarkably good for some time intervals in some regions, yet dismally bad in others, yielding a disjointed and sketchy picture of past life on the continent. Our research into the African Cretaceous is focused on sub-Saharan Africa, a largely tropical to subtropical Precambrian shield area, heavily vegetated for the most part, and deeply weathered, often into fossil-destroying lateritic soils. In this paper we are primarily concerned with two areas of Lower Cretaceous outcrop: one in Cameroon and the other in Malawi. Both are associated with extensional tectonics along reactivated Precambrian mobile belts (Mateer et al., 1992). Our primary objective in this paper is to provide a general comparison between the two; that is, between eastern and western African dinosaur faunas of the Early Cretaceous using the Koum Basin, Cameroon, and the Dinosaur Beds of Karonga, Malawi, as examples (Fig. 1). We will also take this opportunity to examine briefly African Cretaceous dinosaurs and their relationship to those of South America.

Africa became isolated from Madagascar, India, Australia and Antarctica during the Late Jurassic (Pittman et al., 1993). One of the most profound events affecting the physical geography of the Cretaceous world was the opening of the southern Atlantic Ocean by the rifting of South America and Africa. Beginning in the earliest Cretaceous, tectonic rifting that culminated in the isolation of Africa began in the south between the continents. By the Late Albian to Cenomanian the African terrestrial fauna may have been isolated from that of South America by the Atlantic (Pittman et al., 1993). These geographic changes would have precipitated climatic change by modifying oceanic and atmospheric currents distributing heat across the Cretaceous world.

In the Early Cretaceous, volcanism in southern Africa and the reactivation of the Precambrian East African mobile belt resulted in Cretaceous fossil deposits in Malawi, and along the Zambezi River and its tributaries (Eby et al., 1995). Also in the Early Cretaceous, as noted above, on the west side of the continent, South America and Africa were rifting apart along a fault-rift-rift triple junction (Popoff, 1988), completing the Atlantic Ocean by Cenomanian or earlier time.

Thus, the Cretaceous fossil record is largely controlled by the tectonic framework of the continent, which provided the geologic setting in which fossil deposits formed. The chronology of African Cretaceous localities has yet to be documented in detail. Many identifications as presented in the literature are preliminary or based on incomplete material. Table 1 is a compilation of published records of Cretaceous dinosaurs from Africa. This is provided as a guide to published literature only, in recognition of the rather tentative nature of most of the entries.

KOUM BASIN, CAMEROON

The Koum Basin is an isolated basin associated with the Benue Trough, a major structural feature of West Africa (Figs 1, 2). The Benue Trough is an aulacogen, the failed arm of the triple junction that led to the completion of the Atlantic Ocean, extending from the Gulf of Guinea through Nigeria, then dividing into northern and southern branches. The southern branch is called the Yola Arm, which passes into Cameroon. While the Koum Basin is not the only fossiliferous basin associated with the Yola Arm (see also Brunet et al., 1988; Dejax et al., 1989; Michard et al., 1990), it is of interest here because of the dinosaur fauna it contains.

The most complete study of the Koum Basin (also referred to as Mayo Rey Basin in Flynn et al., 1987) and its fauna to date is that of Congleton (1990). The Koum Basin (Figs 2, 3) is an 80km long half-graben oriented east-west, bounded to the north by a fault, and filled with up to 3,000m of fluviatile, overbank, and lacustrine Cretaceous sediments (Tillement, 1971). It is surrounded by Precambrian metamorphic rocks. Cretaceous sediments are exposed primarily along the Mayo Rey, an east to west flowing tributary to the Benue River.

Congleton (1990) referred to the Cretaceous sediments as the Koum Formation, in which he recognised two areally restricted and well-defined members. The Mbissirri Member is composed of reddish fine-grained silty mudstones, clay shales, thin limestones and sandstones. There appear to be cyclical repetitions of cross-bedded sandstones and thicker mudstones within a sequence generally coarsening upwards. Congleton (1990) suggested that the Mbissirri Member represented lacustrine and aggraded meandering stream sediments within a fine-grained meander belt. Carbonised plant fragments, conchostracans, turtle carapace fragments and dinosaur footprint localities (designated KB-3, KB-17, KB-18, KB-23 in Fig. 3) have been found in the Mbissirri Member.

The Mbissirri Member is overlain along the northern margin of the basin by the coarse-grained Grés de Gaba Member. The contact is gradational. The sediments of the Grés de Gaba Member are medium to coarse-grained cross-bedded arkosic sandstones, conglomerates, and interbedded mudstones and palaeosols. Congleton (1990) interpreted the Grés de Gaba Member as representing a coarsegrained, braided fluvial system. Bone-bearing localities (KB-6,

FIG. 1. Location map of Koum Basin, Cameroon and the Dinosaur Beds, Mwakasyunguti area, Karonga, Malawi. Lakes Chad and Malawi indicated in black.

KB-8, KB-13), but no footprints, are known from the Grés de Gaba Member. Congleton et al. (1992) present a section measured at locality KB-6, the most productive bone locality. The base of the locality is coarse sand containing fragmentary scattered bones and teeth representing predominantly, in order of abundance, iguanodontian, theropod and sauropodomorph dinosaurs. One tooth was identified as thyreophoran(?); we consider that identification dubious and the specimen possibly confused with a crocodilian. The iguanodontian teeth resemble those of *Ouranosaurus*. The section fines upwards and small bones, representing particularly anurans and the crocodyliform *Araripesuchus*, but also mammals (Brunet et al., 1990, Jacobs et al., 1988), are concentrated in the lower portion of a mudstone, at the top of which a calcareous palaeosol is developed. Insect trace fossils resembling hymenopteran larval cases are found in the palaeosol. The sequence is succeeded by a coarse sandstone representing the initiation of the next fluvial cycle. A neural arch and neural spine attributed to the region of the sixteenth dorsal vertebra of *Ouranosaurus* (based on height of spine and position of the transverse processes) was found in conglomeratic sandstone at locality KB-13, overlying KB-6 by approximately 5 meters.

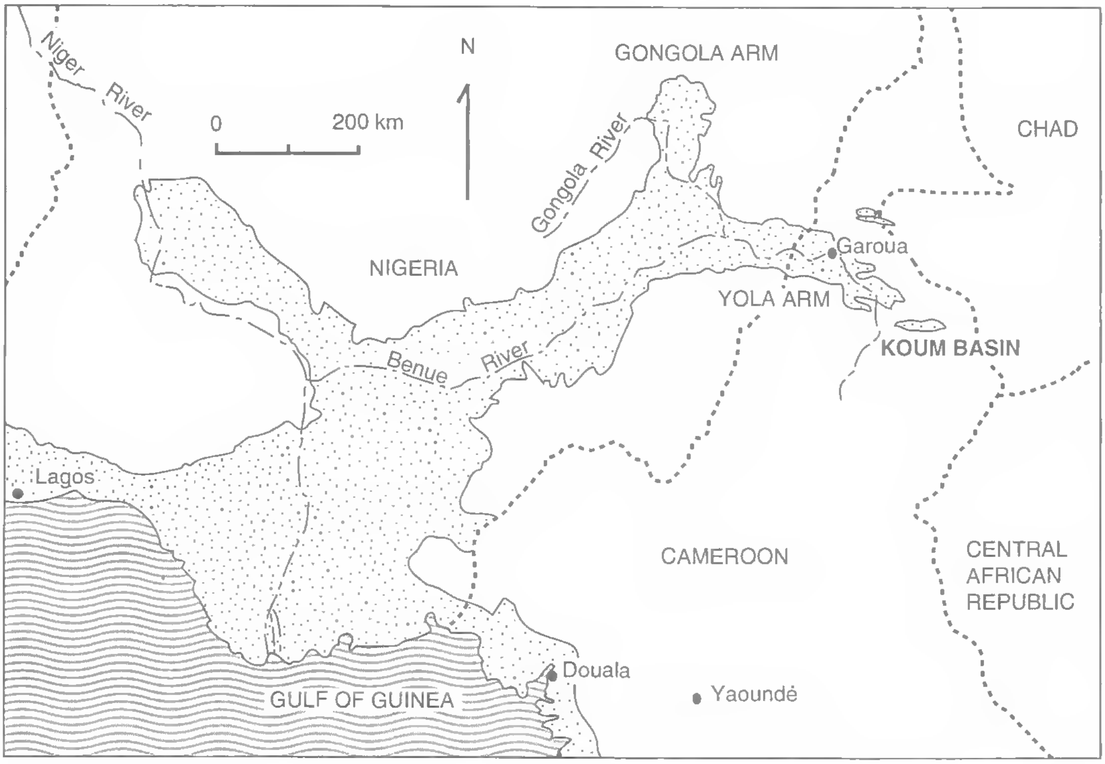

FIG. 2. Distribution of Cretaceous and younger sediments (stippled pattern) in the Benue trough (redrawn from Allix, 1983).

Congleton et al. (1992) suggested that faunas of the Koum Basin were correlative with the locality of Gadoufaoua, Niger, based on the common occurrence of *Araripesuchus* and *Ouranosaurus*. The age of Gadoufaoua is usually considered Aptian (Taquet, 1976). Colin et al. (1992) report the ostracode *Cypridea minuscula* from the Koum Basin (locality KB-24, Mbissirri Member). This genus was originally described from the Candcias Formation, Reconcavo Basin, Brazil. The Candeias Formation is placed within the Rio da Serra local stage (Moura et al., 1994), which ranges from the lower Berriasian to the lower Hauterivian stages (Ponte, 1994). Brunet et al. (1988) estimated the age of the nearby Mayo Oulo Léré Basin to be approximately around the Hauterivian-Barremian transition based on plants, particularly the palynomorph *Dicheiropollis etruscus*. A similar age is suggested for the Babouri-Figil Basin, which also contains dinosaur tracks, for the same reason (Dejax et al., 1989). It appears likely that the Koum Basin is Early Cretaceous in age, no younger than Aptian, but perhaps older.

Dinosaur footprints are relatively abundant in the Koum Basin. Congleton (1990) recognized five morphotypes of tracks corresponding to theropod, ornithopod and sauropod, consistent with incomplete skeletal remains from elsewhere in the basin. The most prolific trackway site is KB-17 in the Mbissirri Member, where tracks occur in four successive sandstone strata. Small theropod prints are the most abundant morphotype. Taken together, the trackways are directed north-northeast or south-southwest consistently, suggesting that the pathways remained constant over the flooding events that deposited the track-bearing strata and that a consistent barrier guided the movements of the dinosaurs.

A considerable amount of variation in stride length and other indicators of relative speed or inferred behavior is reported by Congleton (1990). Interpreted gaits include walking, trotting, sprinting, acceleration, deceleration and hobbling. The majority of the trackmakers appear to have becn walking, however, based on relative stride length and pace angle. Smaller trackmakers appear relatively more energetic than larger

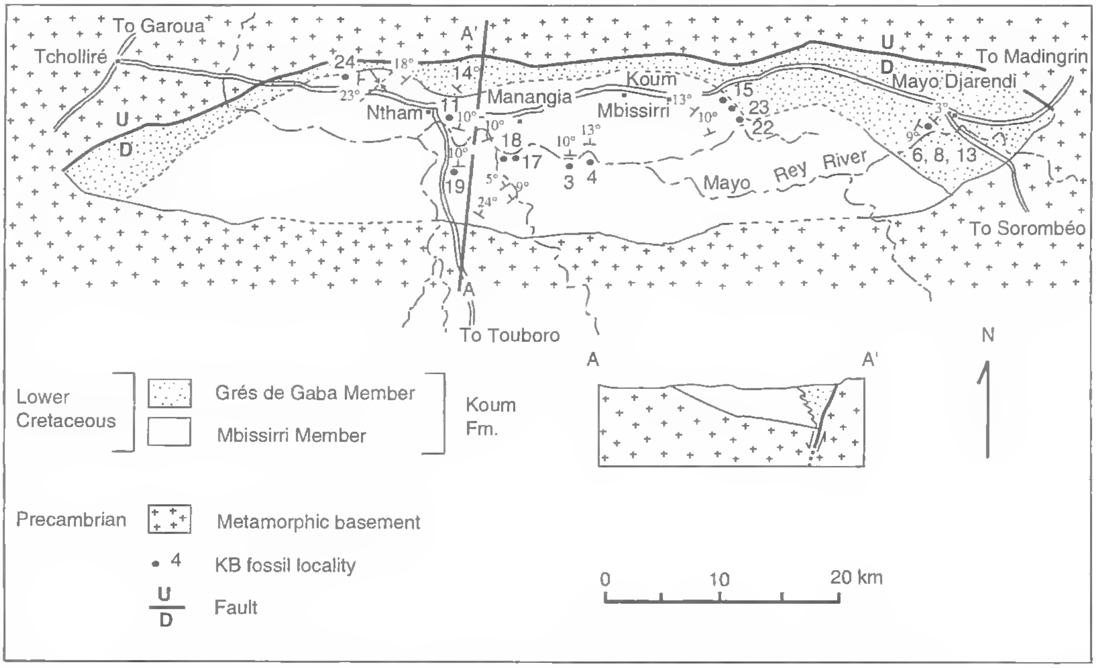

FIG. 3. Geological map of the Koum Basin, northern Cameroon (redrawn from Congleton, 1990).

trackmakers, as interpreted from inferred stride rates.

KARONGA, MALAWI

The Dinosaur Beds of northern Malawi are located along the Sitwe River in the Mwakasyunguti area of Karonga District. Malawi is a long, narrow country located in the southern portion of the East African Rift. Karonga is the northernmost province and Mwakasyunguti is located approximately 70km southwest of Karonga District Headquarters. Jacobs et al. (1992) provided an overview of previous palaeontological research in Malawi.

The Sitwe River near Mwakasyunguti flows through a north-south trending half graben, paralleling the Malawi Rift System (Kaufulu, 1989; Tiercelin et al., 1988) and bordered by Precambrian metamorphic basement. Three sedimentary formations are exposed in the half graben (Fig. 4): the Dinosaur Beds are deposited on the basement and are unconformably overlain by the Plio-Pleistocene Chiwondo Beds, which are in turn unconformably overlain by the Pleistocene Chitemwe Beds.

The Dinosaur Beds are commonly tilted to the northeast with dips ranging from 14-25° northeast. They are cut by two obvious faults (Fig. 4). One fault trends north-south, cutting across almost the entire study area. It juxtaposes sediments of the upper Dinosaur Beds against the lower Dinosaur Beds and the Precambrian basement. Drag on this fault results in southwesterly dips for the upper part of the Dinosaur Beds. The second clearly visible fault cuts across Cretaceous and Cenozoic sediments, juxtaposing the entire package against Precambrian basement.

Dixey (1928; see also Gomani, 1993) divided the Dinosaur Beds into an upper and a lower member based mainly on color. The lower member is unfossiliferous red and purple mud and calcite-cemented sandstone, locally conglomeratic with some mottling and dessication cracks. The upper member is composed primarily of fossiliferous alternating red and white crossbedded fluvial sandstones deposited along braided streams. At least two distinct modes of bone preservation are found in the Dinosaur Beds. Nearly complete and articulated notosuchid crocodyliforms (Clark et al., 1989; Gomani, 1993, in press) are found within burrows in abandoned channel sediments. A more diverse suite of dinosaurs and other taxa occur as isolated bones, associated clusters, or articulated elements in course poorly-sorted sandstone (Gomani, 1993). Plant macrofossils are rare with only two diaspores

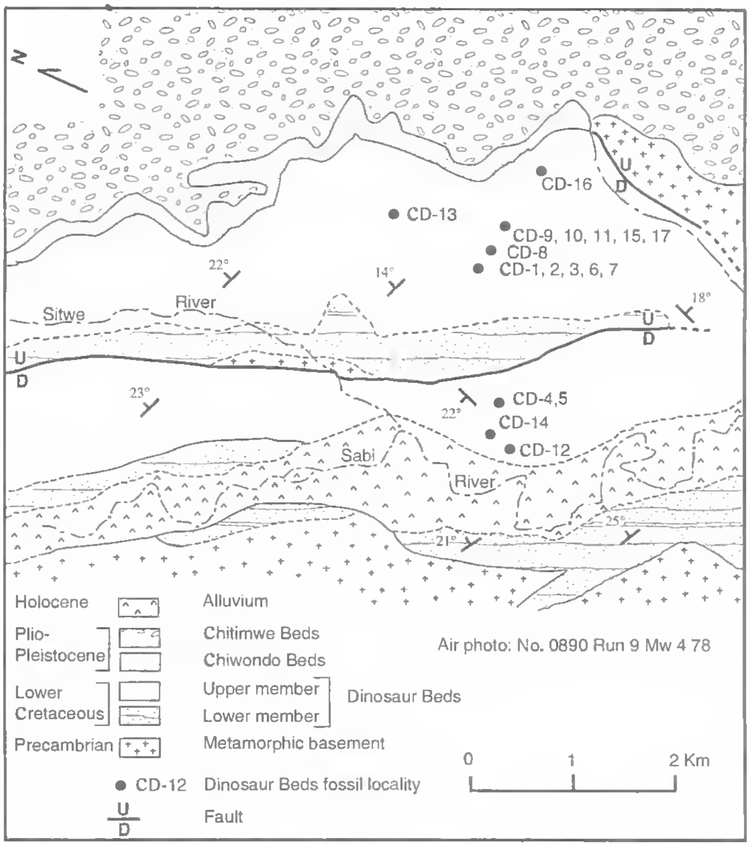

FIG. 4. Geological map of Mwakasyunguti area, Karonga District, Malawi (redrawn from Gomani, 1993).

having been recovered (Jacobs, 1990), and pollen is not preserved. The vertebrate fauna indicates an Early Cretaceous age (Jacobs et al., 1990).

The vertebrate fauna, including fish (but not lungfish), anurans, turtles, crocodyliforms and dinosaurs (Jacobs et al., 1990, 1992; Gomani, 1993), has been collected from localities designated as CD-1 to CD-17 (Fig. 4). Anurans are represented by two skull fragments: one has rugose dermal bones and the other one has no sculpturing (Jacobs et al., 1990). The crocodyliforms include an interesting notosuchid (Gomani, in press), aff. *Araripesuchus* sp., and teeth of an unidentified taxon. Aff. *Araripesuchus* is represented by isolated ziphodont teeth which are indistinguishable from specimens from Cameroon (Congleton, 1990). The latter resemble the type of *Araripesuchus wegeneri* from Niger (Buffetaut, 1981), which Kellner (1994) argues may be generically distinct from the genotypic South American species. The notosuchid species is represented by complete skeletons, which apparently died in burrows (Gomani, in press). It has a long and flat jaw articulation surface and a heterodont dentition with multicusped teeth (Clark et al., 1989; Gomani, in press) that appear to be similar to *Candidodon* from Brazil (Carvalho & Campos, 1988; Carvalho, 1994) and *Chimaerasuchus* from China (Wu et al., 1995). Although distinct, a close phylogenetic relationship of the Malawi notosuchid to *Candidodon* and *Chimaerasuchus* appears likely, but cannot be tested until better material of these genera is found (Gomani, in press). The crus and tarsal bone articulations of the Malawi notosuchid are vertical and the distal condyles of the femur are posteriorly directed. These indicate an erect posture. The ventral position of the occipital condyle and foramen magnum indicates that the head was held perpendicular to the neck (Gomani, in press).

Based on field identifications, it was suggested that the Malawi dinosaur fauna consists of at least five taxa including a titanosaurid, a diplodocid, two morphs of theropods and a stegosaur. However, examination of Argentinean dinosaur specimens and further preparation of the Malawian material necessitate re-evaluation. There are at least two species of sauropods, one of which is *Malawisaurus dixeyi* (Haughton, 1928; Jacobs et al., 1990, 1992, 1993; Gomani, 1993), the other of which is undescribed and has 'pencil-like' teeth. At least two species of theropods are present, based on teeth (Jacobs et al., 1990, 1992). The most abundant elements belong to *Malawisaurus*, a titanosaurid.

Malawisaurus is a titanosaurid because it has a transversely expanded ischium and strongly procoelous anterior caudal vertebrae, derived characters that are considered diagnostic for the Titanosauridae, or possibly a more inclusive monophyletic group containing *Malawisaurus*. Titanosaurids are known to have dermal armor (Depéret, 1896; Bonaparte & Powell, 1980).

Malawisaurus lacks direct evidence of dermal armor, but calcite pseudomorphs shaped like dermal armor were found associated with the bones in the same quarry (Jacobs et al., 1993).

One cervical vertebra referred to *Malawisaurus* (Mal-180, Fig. 5A) has a low neural spine that is not bifurcated. The prezygapophyses extend 10cm beyond the anterior end of the centrum but the postzygapophyses do not extend posteriorly beyond the centrum. The centrum lacks pleurocentral cavities. The cervical ribs are coosified to the centrum and have cranial processes that terminate at the anterior limit of the centrum. The shafts of the ribs extend beyond the centrum posteriorly. In *Saltasaurus loricatus* (PVL 4017-139) of Argentina and in cf. *Titanosaurus* from Brazil (Powell, 1986), the prezygapophyses do not extend beyond the centrum while the postzygapophyses do extend beyond the centrum. In addition, *Saltasaurus* and cf. *Titanosaurus* cervical vertebrae have pleurocentral cavities on the centra. In anterior cervicals of *Saltasaurus* neural spines do not rise above the neural arches while in posterior cervicals low neural spines rise above the neural arches. Based on comparison with *Saltasaurus*, this vertebra of *Malawisaurus* (Mal-180) is probably posterior to the fourth cervical in position.

Dorsal vertebrae attributed to *Malawisaurus* (Mal-181, and Mal-182, Figs 5B-D) indicate no evidence of hyposphene-hypantrum articular surfaces. The centra are opisthocoelous and pleurocoels are anteriorly restricted. The transverse processes of Mal-181 are wide and slightly inclined dorsally. The broad-based, undivided neural spine has elongate anterolateral depressions that are at the same level as the postzygapophyses. A well-developed thin prespinal lamina occurs at the anterior base. The postspinal lamina is thicker than the prespinal lamina.

The base of the undivided neural spine in Mal-182 is narrower than in Mal-181. The prespinal lamina is well-developed. In anterior dorsals (dorsals 1-4) of sauropods the parapophyses are located on the centra while on the posterior dorsals, the parapophyses are high on the centrodiapophysial lamina that extends from the diapophysis (McIntosh, 1990). Mal-181 and Mal-182 are not anterior dorsals because the centra lack parapophyses. In *Epachthosaurus*, the parapophyses become progressively higher posteriorly on dorsals. The transverse processes of Mal-182 are broken, thus the height of the parapophyses and relative vertebral position cannot be determined. The prezygapophyses in Mal-182 are closer together than in Mal-181. The undivided neural spine is high and inclined caudally in Mal-181, but it is vertical in Mal-182. Supradiapophysial laminae in Mal-181 and Mal-182 are well-developed. Deep lateral excavations and high prespinal laminae also occur in *Saltasaurus loricatus*, *Andesaurus delgadoi* and *Argyrosaurus superbus* from Argentina (Bonaparte & Powell, 1980; Calvo & Bonaparte, 1991). In *Saltasaurus*, caudally inclined neural spines occur in more anterior dorsal vertebrae and vertical neural spines occur in posterior dorsal vertebrae (Powell, 1986). Based on comparison with these taxa, Mal-182 probably is more posterior in the vertebral column of *Malawisaurus* than Mal-181.

Caudal vertebrae of *Malawisaurus* are described by Jacobs et al. (1993). The vertebrae progress from procoelous to gently amphicoelous posteriorly. The anterior caudals are strongly procoelous, the prezygapophyses extend slightly beyond the centrum as in *Titanosaurus* sp. from Argentina (Powell, 1986) and *Alamosaurus* from North America (Gilmore, 1946). However, *Alamosaurus* and *Titanosaurus* are more derived because all their posterior caudal vertebrae are procoelous. *Malawisaurus* also shares low caudal neural spines with *Andesaurus* and derived titanosaurids. *Malawisaurus* is distinct from *Andesaurus* and *Epachthosaurus* because these genera have hyposphene-hypantrum articular surfaces on dorsal vertebrae (Calvo & Bonaparte, 1991) that are absent in *Malawisaurus*. All caudal vertebrae of *Epachthosaurus* are procoelous.

Isolated teeth similar to those associated with titanosaurids from Argentina (Huene, 1929 Pl. 1. Figs 12-13; Powell, 1986), Brazil (Kellner, this volume) and to those associated with *Alamosaurus* from North America (Kues et al., 1980; Lucas & Hunt, 1989) occur in the Dinosaur Beds. These teeth are slender and conical. Presence of relatively long slender and conical (peglike) teeth is one of the diagnostic features of Titanosauridae and Diplodocidae (McIntosh, 1990; Titanosauroidea and Diplodocoidea of Upchurch, 1995). Thus, the slender teeth in the Dinosaur Beds may be titanosaurid or diplodocid. The presence of diplodocids in the Dinosaur Beds is suggested by the derived features of an undescribed mandible. It has a short tooth row and the ramus turns at a sharp angle towards the symphysis where the dorsal margin of the mandible flares outward. These characters are also present in South American *Antarctosaurus* (Huene, 1929; Huene & Matley, 1833; Powell,

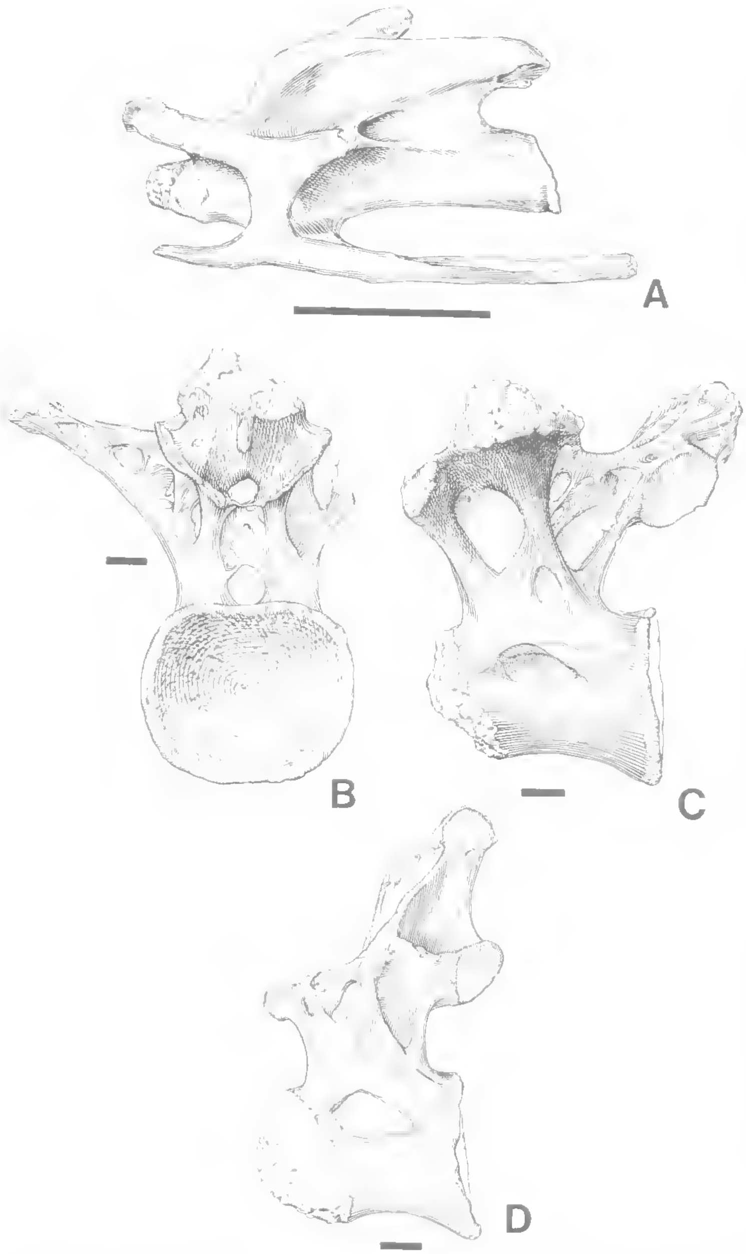

FIG. 5. Vertebrae of *Malawisaurus*. A, middle cervical, Mal-180, left lateral view; scale = 10cm. B, C, D, dorsals of *Malawisaurus* (B, C, Mal-181, right lateral and posterior view, respectively). D, Mal-182, left lateral view. B-D scales = 3cm.

1986). Those authors consider *Antarctosaurus* a titanosaurid, but others have suggested diplodocid or diplodocoid relationships (Jacobs et al., 1993; Hunt et al., 1994; Upchurch, 1994, 1995). While these are given as characters of Diplodocidae (Berman & McIntosh, 1978; Diplodocoidea of Upchurch, 1995), it is clear that the morphological diversity of both South American and African saurpods may be greater than we previously anticipated.

A pelvis from CD-10 is a titanosaurid as suggested by the pelvis of *Epachthosaurus* and *Saltasaurus*. The anterior blade of the ilium of these titanosaurids is curved anterolaterally, a feature that may be derived for this group of sauropods. Further description of the pelvis from Malawi awaits complete preparation.

DISCUSSION AND CONCLUSION

Dinosaurs of Cretaceous age in Africa are widely distributed geographically (Table 1). The data used in the compilation of Table 1 were derived from Broom (1904), Haughton (1928), Dixey & Smith (1929), Dixey (1937, 1939), Greigert et al. (1954), Lavocat (1954), Lapparent (1960), Said (1962), Broin et al. (1971,1974), Kennedy & Klinger (1972), Russell et al. (1976), McLachlan & McMillan (1976), Taquet (1976,1982,1984), El-Khashab (1977), Monbaron (1978), Klitzsch et al. (1979), Pentel'kov & Voronovsky (1979), Sues & Taquet (1979), Dutuit & Ouazzou (1980), Sues (1980), Galton & Coombs (1981), Rich et al. (1983), Cooper (1985), Kent & Gradstein (1985, 1986), William & Savage (1986), Flynn et al. (1987), Handford (1987), Kennedy et al. (1987), Mateer (1987), Shrank (1987), Bouaziz et al. (1988), Brunet et al. (1988), Carroll (1988), Buffetaut (1989a, 1989b), Dejax et al. (1989), Jacobs et al. (1989, 1990, 1992, 1993), Colin & Jacobs (1990), Congleton (1990), Jacobs (1990), Klitzsch & Squyres (1990), Lefranc & Guiraud (1990), Weishampel (1990), Wycisk

(1990), Moody & Sutcliffe (1991), Colin et al. (1992), Congleton et al. (1992), Mateer et al. (1992), Werner (1993a, 1993b), Wescott et al. (1993), Krause & Dodson, (1994); Sereno et al. (1994, 1996), Rauhut & Werner (1995), Forster (1996), Sampson et al. (1996), Krause et al. (in press), and the references therein. The most widely distributed sauropods in Africa are titanosaurids. This is important for palaeobiogeographical comparison between Africa and South America because titanosaurids are also the most widely distributed geographically and most numerous sauropods in South America (Huene, 1929; Huene & Matley, 1933; Bonaparte & Powell, 1980; Powell, 1986; Weishampel, 1990). In Africa, Cretaceous titanosaurids are reported from the Campanian of Madagascar (Russell et al., 1976; Sues & Taquet, 1979; Sues, 1980; Forster, 1996; Sampson et al., 1996; Krause et al., in press), the Senonian of Sudan (Werner, 1993a, 1993b), the Turonian-Santonian of Kenya (Arambourg & Wolff, 1969; Weishampel, 1990; Westcott et al., 1993), the Cenomanian of Egypt (Stromer, 1932), the Albian of Niger (Lapparent, 1960), the Aptian of Malawi (Jacobs et al., 1992, 1993).

Titanosaurid sauropods are clearly important elements in the Cretaceous fauna of both South America and Africa. Titanosaurids are considered to include *Aegyptosaurus*, *Aeolosaurus*, *Alamosaurus*, *Andesaurus*, *Antarctosaurus*, *Argentinosaurus*, *Argyrosaurus*, *Epachthosaurus*, *Hypselosaurus*, *Janenschia*, *Laplatasaurus*, *Macrurosaurus*, *Magyarosaurus*, *Malawisaurus*, *Saltasaurus*, *Titanosaurus* and questionably *Campylodoniscus*. The most diagnostic and most commonly used synapomorphy of titanosaurids is strongly procoelous caudal vertebrae. Having all caudal vertebrae procoelous is derived relative to having posterior caudals amphicoelous.

Malawisaurus has gently amphicoelous posterior caudals. This feature is also seen in *Janenschia* from Tanzania (Janensch, 1922; 1961), *Aeolosaurus rionegrinus* from Argentina (Powell, 1986; 1987) and *Macrurosaurus* from England (Seeley, 1876). No anterior caudal vertebrae are known for *Andesaurus* (Calvo & Bonaparte, 1991). The posterior caudal (Calvo & Bonaparte, 1991, Figs 4A-C) of the latter is described as amphiplatyan. Huene & Matley (1933) described an amphiplatyan posterior caudal and associated it with *Titanosaurus indicus*. The use of the terms gently amphicoelous as compared to amphiplatyan in this case may be a distinction without a difference. Having gently amphicoelous posterior caudal vertebrae may be fairly common among titanosaurids and taxa cannot be excluded from the group because of amphicoelous posterior caudals.

Diplodocids in the Cretaceous of Africa are reported from the Cenomanian of Morocco and the Albian of Niger, Algeria and Morocco (Lavocat, 1954; Lapparent, 1960; Taquet, 1976). These are represented by dorsal vertebrae, humerus, sacrum and teeth of *Rebbachisaurus* and isolated pencil-like teeth (not figured) of an unnamed taxon from Niger (Taquet, 1976). The identification of the unnamed taxon is based on comparison with *Dicraeosaurus* teeth from the Kimmeridgian of Tanzania. Because some pencil-like teeth are referred to titanosaurids, the teeth from Niger require further study for confident assignment to taxon. In the Cretaceous of South America, diplodocids (diplodocoids of Upchurch, 1995) are represented by *Rebbachisaurus* (recently reported by Calvo & Salgado, 1995, in a paper we have not yet had the opportunity to evaluate) and *Amargasaurus* (Salgado & Bonaparte, 1991). *Amargasaurus* is most closely related to the Late Jurassic *Dicraeosaurus* from Tendaguru, Tanzania (Upchurch, 1995). The African titanosaurid *Malawisaurus* is more derived than *Janenschia* from Tendaguru and more similar to South American *Andesaurus*. The undescribed jaw from the Dinosaur Beds of Malawi may be diplodocid but the phylogenetic relationships to other sauropods will be presented elsewhere.

Early Cretaceous sediments and fauna from Cameroon and Malawi are depositionally different and taxonomically distinct. In Cameroon, fossils occur in lacustrine, meanderbelt channel, overbank and braided stream deposits, while in Malawi dinosaur fossils occur predominantly in course-grained, braided fluvial sediments lacking finegrained overbank deposits. Footprints occur in Cameroon but not Malawi. Bones are more complete in Malawi. Cameroon appears to have a more diverse total fauna than Malawi. In Cameroon, the ornithopod *Ouranosaurus* is present while Malawi has no ornithopods. In Malawi, sauropods are the best represented elements, while they are rare in Cameroon. In neither area do we have a reasonably complete understanding of the fauna because of inadequate sampling, but both contribute to the palaeontological baseline for Africa. Compared to other African localities, the Koum Basin appears most similar to Gadoufaoua, Niger, which is close in proximity and probably in age; but neither Koum

TABLE 1. Cretaceous dinosaurs of Africa.

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
Theropoda			
Elaphrosaurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian	Kasr-es-Souk, Morocco (Tegana Fm)	Lapparent, 1960; Monbaron, 1978
Afrovenator	Hauterivian-Barremian	Southern Sahara, Niger	Sereno et al., 1994
Majungasaurus	Campanian-Maastrichtian	Marsa Matruth, Egypt (Phosphatic Beds)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Campanian	Majunga District, Madagascar (Maevarano Fm)	Russell et al., 1976; Sues & Taquet, 1979; Sues, 1980; Foster, 1996; Sampson et al., 1996; Krause et al., in press
Bahariasaurus	Turonian-Santonian	Agadez, Niger (In Beceten Fm)	Greigert et al., 1954; Broin et al., 1974
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Tahoua, Niger (Farak Fm); Northern Province, Sudan (Wadi Milk Fm)	Greigert et al., 1954; Lapparent, 1960; Said, 1962; Taquet, 1976; El-Khashab, 1977; Werner, 1993a
	Albian	Agadez, Niger (Continental Intercalaire)	Lapparent, 1960
Carcharodontosaurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Northern Province, Sudan, (Wadi Milk Fm); Kem Kem, Morocco, (Kem Kem Beds)	Lavocat, 1954; Lapparent, 1960; Said, 1962; El-Khashab, 1977; Werner, 1993a; Sereno et al., 1996
	Albian-Cenomanian	Hammada du Guir, Morocco (Continental Red Beds)	Buffetaut, 1989a, 1989b
	Albian	Tamenghest, Wargla, & Adrar, Algeria; Agadez, Niger (Continental Intercalaire); Kasr-es-Souk, Morocco (Tegana Fm); Gharyan, Libya (Continental Intercalaire) Medenine, Tunisia (Chenini Fm)	Lapparent, 1960; Monbaron, 1978; Bouaziz et al., 1988
	Aptian	Medenine, Tunisia (Chenini Fm)	Bouaziz et al., 1988
Deltadromeus	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Sereno et al., 1996
Spinosaurus	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian-Cenomanian	Hammada du Guir, Morocco (Continental Red Beds)	Buffetaut, 1989a, 1989b
	Albian	Medenine, Tunisia (Chenini Fm)	Bouaziz et al., 1988; Weishampel, 1990
	Aptian	Gadoufaoa, Niger (Elrhaz Fm)	Taquet, 1976; 1982; 1984
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Congleton et al., 1992; Colin et al., 1992
? Spinosaurid indet.	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton 1990; Colin et al., 1992
Dromaeosaurid	Cenomanian	Northem Province, Sudan (Wadi Milk Fm)	Rauhut & Werner, 1995
Theropoda undescribed and indet.	Campanian	Marsa Matruh, Egypt (Nubian sandstone); Majunga District, Madagascar (Maevarano Fm)	Said, 1962; Weishampel, 1990; Forster, 1996; Sampson et al., 1996
	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Albian	Wargla and Adrar, Algeria (Continental Intercalaire); Gharyan, Libya (Continental Intercalaire); Agadez, Niger (Continental Intercalaire); Medenini, Tunisia (Chenini Fm)	Lapparent, 1960; Broin et al., 1971
	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Broin et al., 1974
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Colin et al., 1992
	Barremian	Cape Province, South Africa (Sundays River Fm)	Rich et al., 1983; Weishampel, 1990

TABLE 1 (*cont.*)

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood; Enon Fm)	Rich et al., 1983; Mateer, 1987
Theropod footprints	Maastrichtian	Agadir, Morocco (Unnamed unit)	Weishampel, 1990
	Cenomanian	Laghout, Algeria (Unnamed unit)	Weishampel, 1990
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992; Colin et al., 1992
Sauropoda - Diplodocidae			
cf. *Dicraeosaurus*	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
Rebbachisaurus	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Lavocat, 1954; Sereno et al., 1996
	Albian	Adrar, Wargla and Tamenghest, Algeria (Continental Intercalaire); Agadez, Niger (Continental Intercalaire); Tahoua, Niger (Farak Fm); Kasr-es-Souk, Morocco (Tegana Fm); Medenini, Tunisia (Chenini Fm)	Greigert et al., 1954; Lavocat, 1954; Lapparent, 1960; Taquet, 1976; Monbaron, 1978
Algoasaurus	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Broom, 1904; McLachlan & McMillan, 1976
Diplodocid indet. and undescribed	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984
Titanosauridae			
Titanosaurus	Campanian	Majunga District, Madagascar (Maevarano Fm)	Sues & Taquet, 1979; Sues, 1980; Forster, 1996; Sampson et al., 1996; Krause et al., in press
	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
Aegyptosaurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Tahoua, Niger (Farak Fm)	Greigert et al., 1954; Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian	Agadez, Niger (Continental Intercalaire)	Greigert et al., 1954; Lapparent, 1960; Taquet, 1976
Malawisaurus	Aptian	Karonga, Malawi (Dinosaur Beds)	Haughton, 1928; Jacobs et al., 1990, 1992, 1993
Titanosaurid indet.	Maastrichtian	Agadir, Morocco (Unnamed unit)	Weishampel, 1990
	Campanian	Majunga District, Madagascar (Maevarano Fm)	Suez & Taquet, 1979; Sues, 1980; Forster, 1996
	Santonian	Natal, South Africa (Unnamed unit)	Kennedy et al., 1987
	Turonian-Santonian	Agadez, Niger (Unnamed unit);	Broin et al., 1974
	Cenomanian	Northern Province, Sudan (Wadi Milk Fm)	Schrank, 1987; Werner, 1993a; 1993b; Rauhut & Werner, 1995
	Aptian	Agadez, Niger (In Beceten Fm); Gadoufaoa, Niger (Elrhaz Fm)	Greigert et al., 1954; Broin et al., 1974; Taquet, 1976, 1982
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Forster, 1996
Brachiosauridae			
Brachiosaurus	Albian	Wargla and Adrar, Algeria (Continental Intercalaire)	Lapparent, 1960
?Pleurocoelus	Albian	Agadez, Niger (Continental Intercalaire)	Lapparent, 1960
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	McLachlan & McMillan, 1976; Rich et al., 1983
Brachiosaurid indet.	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Forster, 1996
Camarasauridae			
Camarasaurid indet.	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Rich et al., 1983

TABLE 1 (*cont.*)

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
Sauropoda indet. and undescribed	Turonian-Santonian	Rift Valley Province, Kenya (TurkanaGrits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Madagascar (Ankarafantsika Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977; Mateer et al., 1992
	Albian	Adrar, Algeria (Continental Intercalaire and Unnamed unit); Medenine, Tunisia (Chenini Fm); Gao, Mali (Continental Intercalaire)	Lapparent, 1960; Broin et al., 1971; Bouaziz et al., 1988
	Aptian	Karonga, Malawi (Dinosaur Beds); Chirunda Hill, Mozambique (Lupata Series); Luangwa Valley, Zambia (Dinosaur Beds)	Dixey & Smith, 1929; Dixey, 1937, 1939; Pentel'kov &Voronovsky, 1979; Colin & Jacobs, 1990; Jacobs et al., 1990, 1992, 1993
	Barremian-Aptian	Mayo Djarendi, (Koum Basin)	Brunet et al., 1990
	Hauterivian-Barremian	Southem Sahara, Niger	Sereno et al., 1994
Sauropod footprints	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992
	Tithonian-Berriasian	Marrakech, Morocco (Unnamed unit)	Dutuit & Ouazzou, 1980
Ornithopoda - Iguanodontidae			
Ouranosaurus	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin); Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984; Brunet et al., 1990; Congleton, 1990; Congleton et al., 1992
Iguanodontian indet.	Cenomanian	Northem Province, Sudan (Wadi Milk Fm); Kem Kem, Morocco, (Kem Kem Beds)	Rauhut & Werner, 1995; Sereno et al., 1996
	Aptian	Medenini, Tunisia (Continental Intercalaire); Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Rich et al., 1983; Foster, 1996
Hypsilophodontidae			
Valdosaurus	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984
Kangnasaurus	Tithonian-Hauterivian	Cape Province, South Africa (Kalahari Deposits)	Cooper, 1985
Hypsilophodontid indet.	Cenomanian	Northem Province, Sudan (Wadi Milk Fm)	Rauhut & Wemer, 1995
Ornithopoda indet.	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Northem Province, Sudan (Wadi Milk Fm)	Werner, 1993a; Rauhut & Werner, 1995
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	McLachlan & McMillan, 1976
Ornithopod footprints	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Sereno et al., 1996
	Barremian-Aptian	Mayo Djarendi (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992
? Pachycephalosauria - ?Pachycephalosauridae			
Majungatholus (? = *Majungasaurus*)	Campanian	Majunga District, Madagascar (Maevarano Fm)	Sues & Taquet, 1979; Sues, 1980; Sampson et al., 1996a,b; Krause et al., in press
Thyreophora - Stegosauridae			
Paranthodon	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Galton & Coombs, 1981; Rich et al., 1983
Nodosauridae			
Nodosaurid indet.	Albian	Gao, Mali; Agadez, Niger (Continental Intercalaire)	Lapparent, 1960; Weishampel, 1990
? Thyreophora indet.	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Congleton et al., 1992

nor the Dinosaur Beds of Malawi can be shown to be particularly similar to other African localities. This is interesting with respect to the differentiation and development of endemism in the African dinosaur fauna in that it highlights both the chronological and geographic shortcomings of the record as we now know it.

Ongoing work by groups of researchers in the Sahara, southeast Africa and Madagascar is elucidating further the history of dinosaurs on this great continent. For example, Sereno et al. (1994) described the theropod *Afrovenator*, a tetanuran more primitive than *Spinosaurus*, and mentions sauropod remains with unclear affinities, but not diplodocid or titanosaurid, from the Early Cretaceous of Niger. The bones were found in channel fills and show evidence of fluvial transport. They interpret the area to have had a uniform climatic regime because of the absence of caliche and fossil wood without growth rings. Work in the Cenomanian of Morocco (Sereno et al., 1996) led to the discovery of the coelurosaur *Deltadromeus* and the description of the skull of the large allosauroid *Carcharodontosaurus*. Sereno et al. (1996) and Sereno (1996) concluded that dinosaurian endemism began abruptly in the Late Cretaceous.

Late Cretaceous work in Madagascar recently by field parties led by David Krause have resulted in significant new discoveries, particularly of titanosaurids, the theropod *Majungasaurus* and birds. These discoveries, and the ones that are sure to follow, may prove to be particularily enlightening because Madagascar remained joined to the Gondwana landmass including India, Australia, Antarctica and South America into the Early Cretaceous, long after it had rifted from the west coast of Africa (Krause & Dodson, 1994; Forster, 1996; Sampson et al., 1996; Krause et al., in press).

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